

A Brief Chronicle of the Genus *Cordyceps* Fr., the Oldest Valid Genus in Cordycipitaceae (Hypocreales, Ascomycota)

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Abstract The earliest pre-Linnaean fungal genera are briefly discussed here with special emphasis on the nomenclatural connection with the genus *Cordyceps* Fr. Since its valid publication under the basidiomycetous genus *Clavaria* Vaill. ex L. (*Clavaria militaris* L. Sp. Pl. 2:1182, 1753), the genus *Cordyceps* has undergone nomenclatural changes in the post-Linnaean era, but has stood firmly for approximately 200 years. Synonyms of *Cordyceps* were collected from different literature sources and analyzed based on the species they represent. True synonyms of *Cordyceps* Fr. were defined as genera that represented species of *Cordyceps* Fr. emend. G. H. Sung, J. M. Sung, Hywel-Jones & Spatafora. The most common synonyms of *Cordyceps* observed were *Clavaria* and *Sphaeria* Hall, reported in the 18th and in the first half of the 19th century, respectively. *Cordyceps*, the oldest genus in the *Cordyceps* s. s. clade of Cordycipitaceae, is the most preferred name under the “One Fungus = One Name” principle on priority bases.

Keywords *Elaphocordyceps*, Fungal taxonomy, *Metacordyceps*, One Fungus = One Name, *Ophiocordyceps*

EARLY FUNGAL GENERA

In the 16th century, *Fungus* Tourn. ex Adans. and *Tuber* P. Micheli ex F. H. Wigg. were the only two generic fungal names (Table 1) [1]. At that time, fungi were considered as nothing more than the superfluous humidity of soil, trees, rotten wood, and other decaying substances [2]; in fact,

potatoes and legume root nodules were considered to be relatives of truffles [3]. At the end of the 17th century and the beginning of the 18th century, Tournefort (1656–1708), considered the father of the modern generic concept, added five new fungal genera, including *Agaricus* L. of Bauhin (Table 1) [2, 4, 5], which were studied by successive authors of the early 18th century (Table 1) [6–8]. Subsequently, approximately 30 new fungal genera were proposed by Micheli [9], the father of mycology, which were studied by Von Haller [10, 11] who added the new genera to the list (Table 2). According to some authors [9, 12–15], *Cordyceps militaris* (L. : Fr.) Fr., the type species of *Cordyceps* Fr., was already described in the 17th and early 18th century literature under old generic names, including: *Funguli clavati; ex gracili caule paulatim crassiores reddit;* *ad digit minimi fere longitudinem pallid accedentes* (tentative translation: clavate, slender, gradually broadening, somewhat longitudinally similar to finger or toe, pale toward tip) [16, 17]; *Fungus parvus luteus ad ophioglossoiden nigrum accedens* (tentative translation: small, yellow, tongue-like, black toward tip) (common English name: yellow adders-tongue mushroom) [18, 19]; and *Fungoides clavatum minus* [6].

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Table 1. Early fungal genera

	De Lobel [1]	Bauhin [2]	De Tournefort ^a [4]	De Tournefort [5]	Dillen [6]	Buxbaum [7]	Vaillant [8]
Genera	Fungus	Fungus	Fungus	Fungus	-	Fungus	Fungus
	-	-	-	Fungoides	Fungoides	Fungoides	Fungoides
	-	-	-	-	Peziza	-	-
	-	-	Boletus	Boletus	Boletus	Boletus	Boletus
	-	Agaricus	Agaricus	Agaricus	Agaricus	Agaricus	Agaricus
	-	-	Lycoperdon	Lycoperdon	-	Lycoperdon	Lycoperdon
	-	-	Coralloides	Coralloides	-	Coralloides	Coralloides
Tubera	Tuber	Tubera	Tubera	Tubera	Tuberum	Tubera	Tubera
	-	-	-	-	-	-	Clavaria
	-	-	-	-	-	Byssus	-
	-	-	-	-	Phallus	-	-
	-	-	-	-	Amanita	-	-
	-	-	-	-	Morchella	-	-
	-	-	-	-	Erinaceus	-	-

^aFungal groups described under each genus are as follows (in parenthesis): *Fungus* (agaricus, boletus), *Boletus* (morels, clathrus, and phal-lus), *Agaricus* (polypores, bracket fungi), *Lycoperdon* (puff-balls), *Coralloides* (clavarioid forms), and *Tubera* (truffles).

OTHER GENERIC NAMES FOR CORDYCEPS FR.

Vaillant [8] reserved the name *Coralloides* Tourn. for branched forms and erected a new genus, *Clavaria* Vaill. ex L., for unbranched species that also included *Cordyceps militaris* (L. : Fr.) Fr. (as *Clavaria militaris, crocea* Vaill.), thus becoming the first extant generic name used for *Cordyceps* s. l. *Clavaria* became such a popular name for basidiomycetous genera that throughout the 18th century it was commonly used for several species of *Cordyceps* s. l. such as *Clavaria capitata* Holmsk. and *Clavaria pileata* Retz. for *Cordyceps capitata* (Holmsk.) Link (current name *Elaphocordyceps capitata* (Holmsk.) G. H. Sung et al.); *Clavaria lutea minima* Mich., *Clavaria militaris* L., *C. lavaria simplex oblonga pulvinata* Schmidel, *Clavaria squamosa* Lam., and *Clavaria granulosa* Bull. for *Cordyceps militaris*; and *Clavaria parasitica* Willd. and *Clavaria radicosa* Bull. for *Cordyceps ophioglossoides* (Ehrh.) Link (current name *Elaphocordyceps ophioglossoides* (Ehrh.) G. H. Sung et al.); and *Clavaria sobolifera* Hill ex Watson for *Cordyceps sobolifera* (Hill ex Watson) Berk. & Broome (current name *Ophiocordyceps sobolifera* (Hill ex Watson) G. H. Sung et al.). However, Buxbaum [12] retained the genus name *Coralloides* Tourn. for *Cordyceps*, e.g., *Coralloides clavata, lutea, minor* was used for *Cordyceps militaris*.

Von Haller [11] established a new ascomycetous genus, *Sphaeria* Hall., to distinguish species with rounded, entire perithecia, furnished at the apex with a minute orifice, and asci converging and dissolving at length. Based on these characteristics, several *Cordyceps* species s. l. were transferred from *Clavaria* into *Sphaeria* thus departing from the traditional basidiomycetous classification, including: *Sphaeria agariciformis* Bolton/S. *capitata* (Holmsk.) Pers. (= *Cordyceps capitata*, current name *Elaphocordyceps capitata*); *S. entomorrhiza* Dicks. (= *Cordyceps entomorrhiza* (Dicks.) Fr., current name *Ophiocordyceps entomorrhiza* (Dicks.) G. H. Sung et al.); *S. gunnii* Berk. (= *Cordyceps gunnii* (Berk.)

Berk.); *S. huegelii* Corda/S. *larvarium* Westwood (≡ *Cordyceps huegelii* Corda, current name *Ophiocordyceps larvarium* (Westwood) G. H. Sung et al.); *S. innominata* R. Taylor/S. *taylorii* Berk. (= *Cordyceps taylorii* (Berk.) Sacc., current name *Ophiocordyceps taylorii* (Berk.) G. H. Sung et al.); *S. robertsii* Hook. (= *Cordyceps robertsii* (Hook.) Berk., current name *Ophiocordyceps robertsii* (Hook.) G. H. Sung et al.); *S. militaris* (L.) J. F. Gmel. (= *Cordyceps militaris*); *S. ophioglossoides* J. F. Gmel. and *S. radicosa* De Candolle (= *Cordyceps ophioglossoides*, current name *Elaphocordyceps ophioglossoides*); *S. sinensis* Berk. (= *Cordyceps sinensis* (Berk.) Sacc., current name *Ophiocordyceps sinensis* (Berk.) G. H. Sung et al.); *S. sobolifera* (Hill ex Watson) Berk. (= *Cordyceps sobolifera*, current name *Ophiocordyceps sobolifera*); and *S. sphecocephala* Klotzsch ex Berk. (= *Cordyceps sphecocephala* (Klotzsch ex Berk.) Berk. & M. A. Curtis, current name *Ophiocordyceps sphecocephala* (Klotzsch ex Berk.) G. H. Sung et al.). By the early 19th century, *Sphaeria* had already become a large genus consisting of more than 500 species, necessitating its division into Sections, Tribes, and Series [20].

ORIGIN OF THE GENUS NAME CORDYCEPS AND ITS SYNONYMS

Cordyceps was first coined as a genus in *Pyrenomyctetes* by Fries [21] from a combination of the Greek word *cordyle*, meaning a club, and the Latin word *caput*, meaning a head. However, Fries [20] himself downgraded *Cordyceps* to the tribe level of *Sphaeria* and described it as *stroma erectum, caulescens, simplex, ramosum, imarginatum, stipite sterili suffultum, perithecia peripherica, demum prominentia, ostiolis aequalibus* (tentative translation: having erect stroma with a simple or branching stem, a sterile stalk supporting the perithecia at the periphery, and projecting with openings at the apex). The treatment of Fries [20] was soon reversed by Link [22], who reaffirmed the genus-level status of

Table 2. Major fungal genera of Micheli [9] and Von Haller [10, 11]

	Micheli [9]	Von Haller [10]	Von Haller [11]
Genera	Fungus	Fungus	-
<i>Fungoides</i>			-
		<i>Peziza</i>	<i>Peziza</i>
<i>Boletus</i>		<i>Boletus</i>	<i>Boletus</i>
		<i>Agaricus</i>	-
<i>Lycoperdon</i>		<i>Lycoperdon</i>	<i>Lycoperdon</i>
<i>Coralloides</i>		<i>Coralloides</i>	<i>Clavaria</i>
<i>Tuber</i>		<i>Tuber</i>	-
<i>Clavaria</i>		<i>Clavaria</i>	<i>Clavaria</i>
<i>Botrytis</i>		<i>Botrytis</i>	<i>Botrytis</i>
<i>Aspergillus</i>		<i>Aspergillus</i>	<i>Aspergillus</i>
<i>Polyporus</i>		<i>Polyporus</i>	<i>Polyporus</i>
<i>Geaster</i>		<i>Geaster</i>	-
<i>Lycogala</i>		<i>Lycogala</i>	<i>Lycogala</i>
<i>Clathroidastrum</i>		<i>Clathroidastrum</i>	-
<i>Clathroides</i>		<i>Clathroides</i>	<i>Trichia</i>
<i>Lycoperdoides</i>		<i>Lycoperdoides</i>	-
<i>Carpobolus</i>		<i>Carpobolus</i>	-
<i>Lycoperdastrum</i>		<i>Lycoperdastrum</i>	-
<i>Puccinia</i>		<i>Puccinia</i>	<i>Puccinia</i>
<i>Cyathoides</i>		<i>Cyathoides</i>	<i>Cyathus</i>
<i>Suillus</i>		<i>Suillus</i>	-
<i>Fungoidaster</i>		<i>Fungoidaster</i>	<i>Agaricum</i>
<i>Byssi</i>		<i>Byssus</i>	<i>Byssus</i>
		<i>Mucilago</i>	<i>Mucilago</i>
<i>Phallus</i>		<i>Phallus</i>	<i>Phallus</i>
<i>Clathrus</i>		-	-
<i>Mucor</i>		<i>Mucor</i>	<i>Mucor</i>
			<i>Tremella</i>
			<i>Amanita</i>
<i>Erinaceus</i>		<i>Erinaceus</i>	<i>Echinus</i>
		<i>Embolus</i>	-
		<i>Sphaerocephalus</i>	-
		<i>Buxbaumia</i>	-
		<i>Agarico-Polyporus</i>	-
		<i>Agarico-Suillus</i>	-
		<i>Echin-Agaricus</i>	-
		<i>Merulius</i>	-
		<i>Agarico-Merulius</i>	-
		<i>Agarico-Fungus</i>	-
			<i>Conferua</i>
			<i>Ulva</i>
			<i>Fuligo</i>
			<i>Embolus</i>
<i>Lichen-Agaricus</i>		-	<i>Sphaeria</i>
<i>Ceratospermum</i>		-	<i>Ceratospermum</i>
		-	<i>Merulius</i>

Cordyceps. However, the treatment of Fries [20] had such a profound effect on taxonomists that *Cordyceps* species were named under *Sphaeria* for many decades.

The genus *Cordyceps* was first conserved in the Seattle Code (1972) with citation *Cordyceps* (E. M. Fries) Link, Handb. 3: 346 (1833). However, in subsequent Botanical Codes, citations for *Cordyceps* differed from *Cordyceps* E. M. Fries, Observ. Mycol. 2: 316 (1818, cancel page) in

Sydney Code (1983) to *Cordyceps* Fr., Observ. Mycol. 2 (revis.): 316 (1824) in Tokyo Code (1994) [23]. The citation of the genus *Cordyceps* in the Sydney Code is considered to be correct, i.e., *Cordyceps* Fr., Observ. Mycol. 2(revis.): 316, 1818, nom. cons. [23-25].

Type species: *Cordyceps militaris* (L. : Fr.) Fr., Observ. Mycol. 2(revis.): 317 (1818).

The phylogenetic clade of *Cordyceps* s. s. was recently delimited [25]. Nearly 20 different genera have been reported as synonyms of *Cordyceps* Fr. in various sources (<http://www.speciesfungorum.org>, <http://www.mycobank.org>, <http://www.cybertruffle.org.uk>). We recognize only those genera that represent *Cordyceps militaris* or any other *Cordyceps* species in the clade *Cordyceps* s. s. of Sung *et al.* (for instance *C. tuberculata*) as true synonyms of *Cordyceps* Fr., [25] and they are listed below.

Cordyceps Fr.

- ≡ *Clavaria* Vaill. ex L., Sp. Pl. 2: 1182 (1753).
- ≡ *Sphaeria* Hall., Hist. Stirp. Helv. 3: 120 (1768).
- ≡ *Hypoxyllum* Juss., Gen. Pl.: 6 (1789).
- ≡ *Cordylia* Fr., Observ. Mycol. 2(original): 316 (1818), nom. illegit., non Pers. (1807) [Caesalpiniaceae].
- ≡ *Xylaria* Hill ex Grev., Scott. Crypt. Fl. (Edinburgh) 2: 2 (1823).
- ≡ *Corynesphaera* Dumort., Comment. Bot. (Tournay): 92 (1822).
- ≡ *Sphaeria* "trib." *Cordyceps* (Fr.: Fr.) Fr., Syst. Mycol. 2: 323 (1823).
- ≡ *Kentrosporium* Wallr., Beitr. Bot. 1: 163 (1844).
- ≡ *Akrophyton* Lebert, Z. Wiss. Zool. (Leipzig) 9: 449 (1858).
- ≡ *Torrubia* Lév., in Cesati & de Notaris, Comm. Soc. crittog. Ital. 1: 192 (1863).
- ≡ *Phytocordyceps* C. H. Su & H. H. Wang, Mycotaxon 26: 338 (1986).

However, we do not recognize the following genera as true synonyms of *Cordyceps* s. s. [25]:

Mitrasphaera Dumort., Comment. Bot. (Tournay): 92 (1822).

Cordyliceps Fr., 1832.

Campylothecium Ces., 1846.

Polistophthora Lebert, Z. Wiss. Zool., (Leipzig) 9: 452 (1858).

Racemella Ces., Comm. Soc. crittog. Ital. 1: 65 (1861).

Tettigorhyza G. Bertol., Mem. R. Accad. Sci. Ist. Bologna, Ser. 3 5: 574 (1875).

Campylothecium Ces. represented *Cordyceps myrmecophila* Ces., *Polistophthora* Lebert represented *Cordyceps sphecocephala*, and *Racemella* Ces. represented *Cordyceps robertsii*, all of which are now transferred to the new genus *Ophiocordyceps* Petch emend. G. H. Sung *et al.* (*Ophiocordycipitaceae* G. H. Sung *et al.*) [25]. Similarly, *Mitrasphaera* Dumort. represented *Cordyceps capitata* that is now transferred to a new genus, *Elaphocordyceps* G. H. Sung & Spatafora (*Ophiocordycipitaceae*) [25]. *Tettigorhyza*

G. Bertol. and *Cordyliceps* Fr. are not considered true synonyms as it is not clear which *Cordyceps* species they represent.

SUBGENERIC CLASSIFICATIONS AND AMENDMENT OF CORDYCEPS

As the number of species of *Cordyceps* s. l. increased, successive authors began arranging the genus on the basis of host and morphological characters. Here, the era of subgeneric classification of *Cordyceps* is tentatively divided into so-called artificial and natural classifications that correspond to the 19th and 20th century, respectively, although it is difficult to make a clear demarcation line.

Artificial classification. The insect/fungal host, shape of the stromata, and position of the perithecia were the principal characters used for the subgeneric classifications of *Cordyceps* s. l. in the 19th century (Table 3). Some of the major works under this system are mentioned here. Wallroth [26] seemingly organized entomophyte species of *Cordyceps* s. l. (under *Kentrosporium* Wallr.) into *capitata* (*stromate sphaerico*, 3 spp.) and *clavata* (*stromate clavato*, 2 spp.). Fries [27] included both entomogenous and mycogenous species in *Cordyceps* and divided them into *Entomogenae* (2 spp.) and *Mycogenae* (2 spp.), solely based on the nature of the host. Tulasne and Tulasne [28] classified *Cordyceps* species under a different genus, *Torrubia* Lév., into *Entomogenae* (8 spp.) and *Mycogenae* (2 spp.), which were further subclassified, depending on the shape of the stroma, into *Clavatae* (3 spp.) and *Capitatae* (5 spp.), and *Claviformes* (1 sp.) and *Capitatae* (1 sp.), respectively. In slight contrast to preceding authors, Saccardo [29] classified *Cordyceps* species into three main groups: *Eucordyceps* Sacc. (entomogenous with immersed perithecia, 21 spp.), *Racemella* Ces. (entomogenous with superficial perithecia, 7 spp.), and *Cordylia* Tul. (mycogenous with immersed perithecia, 2 spp.). Cooke [30] based his classification of

entomogenous species of *Cordyceps* on the stroma shape and branching pattern: capitulum globose or elliptical (18 spp.); stroma furcate, capitulum subglobose (3 spp.); stroma simple, clubs elongated (14 spp.); stroma furcate, clubs elongated (4 spp.); and clubs various, perithecia free (6 spp.).

None of the former authors designated the divisions or groups of *Cordyceps* as subgenera. It was Schroeter [31] who formally ranked the divisions of *Cordyceps* (under *Torrubia* Lév.) into the subgenera *Racemella* Ces. (species with perithecia partly embedded, 4 spp.) and *Cordylia* Tul. (both entomogenous and mycogenous species having entirely embedded perithecia, 4 spp.), and then further divided *Cordylia* into *Eucordyceps* Sacc. (entomogenous, 2 spp.) and *Cordylia* Tul. (mycogenous, 2 spp.) (Table 3). Massee [32], however, only recognized entomogenous species under *Cordyceps* and transferred any mycogenous species to *Cordylia* sensu Tul. He refrained from subgeneric classification of *Cordyceps*, but rather separated the species based on perithecial position such as *perithecia entirely or partly immersed* (40 spp.) and *perithecia superficial* (12 spp.) as well as on the septation of ascospores (Table 3). Broadly arranging *Cordyceps* species by the host type, Lindau [33] established two subgenera, *Eucordyceps* Lindau (16 spp.) for entomogenous species and *Cordylia* Tul. (2 spp.) for mycogenous species. From Table 3, it can be observed that in the 19th century there were sporadic tendencies of recognizing only entomogenous species under *Cordyceps* [26, 32, 34], although these tendencies were almost completely abandoned by the 20th century.

Natural classification. By the middle of the 19th century, microscopic details of fructifications in *Cordyceps* species had been observed, such as the number of ascospores in an ascus; the mode of arrangement of ascospores in the ascus in one or two rows or in a crowded or irregular manner; the shape and color of ascospores; septation either unicellular and simple or divided by

Table 3. Subgeneric classifications^a of *Cordyceps s. l.* in the 19th century

Wallroth [26]	Fries [27]	Tulasne and Tulasne [28]	Saccardo [29]	Roumeguère [34]	Schroeter [31]		Massee [32]	Lindau [33]
Groups/ Subgenera	<i>capitata</i> (3 ^b)	<i>Entomogenae</i> (2)	<i>Entomogenae</i> (8)	<i>Clavatae</i> (3) Sacc. (21)	<i>Eucordyceps</i> (21)	<i>Eucordyceps</i> Ces. (4)	<i>Racemella</i> <i>Perithecia</i> entirely/partly immersed (40)	<i>Spores</i> septate (38)
								<i>Eucordyceps</i> Lindau (16)
								<i>Spores</i> continuous (2)
<i>clavata</i> (2)			<i>Capitatae</i> (5) Ces. (7)	<i>Racemella</i> Ces. (7)	<i>Racemellae</i> (7)	<i>Cordylia</i> Tul. (4)	<i>Eucordyceps</i> Sacc. (2)	<i>Perithecia</i> superficial (12) <i>Spores</i> septate (11)
								continuous (1)
	<i>Mycogenae</i> (2)	<i>Mycogenae</i> (2)	<i>Claviformes</i> (1)	<i>Cordylia</i> Tul. (2)		<i>Cordylia</i> Tul. (2)		<i>Cordylia</i> Tul. (2)
			<i>Capitatae</i> (1)					

^aDelimitation of similar subgenera may differ from author to author.

^bNumber of species are shown in parentheses.

Table 4. Major subgeneric classifications^a of *Cordyceps s. l.* in the 20th century.

Kobayasi [37]	Mains [38]	Moureau [39]	Koval [40, 41]	Kobayasi [42]
Subgenera				
<i>Ophiocordyceps</i> (Petch) Kobayasi (15 ^b)	<i>Ophiocordyceps</i> (Petch) Kobayasi (1)	<i>Ophiocordyceps</i> Petch (1)	<i>Ophiocordyceps</i> Petch (10)	<i>Ophiocordyceps</i> (Petch) Kobayasi (19)
<i>Eucordyceps</i> Kobayasi (116)	<i>Cordyceps</i> (33)	<i>Eucordyceps</i> Lindau (34)	<i>Cordyceps</i> Kobayasi (43)	<i>Eucordyceps</i> Kobayasi (255)
<i>Neocordyceps</i> Kobayasi (6)			<i>Neocordyceps</i> (Kobayasi) Koval (2)	<i>Neocordyceps</i> Kobayasi (8)
	<i>Cryptocordyceps</i> Mains (1)			
	<i>Racemella</i> (Ces.) Sacc. (6)			
		<i>Torrubiella</i> Boud. (2)		
			<i>Fusicordyceps</i> Koval (10)	

^aDelimitation of similar subgenera may differ from author to author.

^bNumber of species are shown in parentheses.

transverse, transverse and longitudinal, or even oblique septa; and ascospore length [35]. Tulasne and Tulasne [28] and others also investigated the micro-characters of the *Cordyceps* species; however, such micro-characters were barely utilized in subgeneric classifications of *Cordyceps* (Table 3).

The use of micro-characters for subgeneric classification of *Cordyceps* can largely be accredited to T. Petch, E. B. Mains, and Y. Kobayasi in the 20th century (Table 4). Despite his contribution to the description of over 150 species of *Cordyceps* spanning over three decades in the first half of the 20th century, Petch [36] did not produce his own classification. The exception is the establishment of a new genus, *Ophiocordyceps* Petch, that he erected to accommodate *Cordyceps* species with non-fragmenting ascospores [36]. The genus was not recognized by later authors; however, it was recently reinstated and emended, based on the phylogenetic classification of *Cordyceps s. l.* [25]. In the history of *Cordyceps* taxonomy, the most detailed revisionary work was conducted by Kobayasi [37], who recognized three subgenera: *Ophiocordyceps* (Petch) Kobayasi (having non-fragmenting ascospores) (15 spp.), *Eucordyceps* Kobayasi (entomogenous and mycogenous species having fragmenting ascospores) (116 spp.), and *Neocordyceps* Kobayasi (having obliquely oriented perithecia) (6 spp.). He further classified these subgenera into 5 sections and 11 subsections in total, which can be considered as a workable natural classification of *Cordyceps*. Other mycologists contributed revisions to *Cordyceps* classification based on regional distributions (Table 4). For example, based on the North American species, the genus *Cordyceps* was divided into four subgenera: *Racemella* (Ces.) Sacc. (perithecia superficial and free) (6 spp.), *Cordyceps* (perithecia partly or completely immersed) (33 spp.), *Cryptocordyceps* Mains (perithecia developing in a palisade-like layer) (1 sp.), and *Ophiocordyceps* (Petch) Kobayasi (1 sp.), of which the subgenus *Cordyceps* was further divided into four sections [38]. In a somewhat similar manner [37], Moureau [39] recognized three subgenera in *Cordyceps* based on

African species: *Torrubiella* Boud. (2 spp.), *Eucordyceps* Lindau (34 spp.), and *Ophiocordyceps* Petch (1 sp.). Koval [40, 41] divided *Cordyceps* into four subgenera: *Ophiocordyceps* Petch (10 spp.), *Cordyceps* Kobayasi (43 spp.), *Fusicordyceps* Koval (10 spp.), and *Neocordyceps* (Kobayasi) Koval (2 spp.), which were further classified into nine sections. Kobayasi [42], in his second revision of *Cordyceps*, retained his previous three subgenera *Ophiocordyceps* (19 spp.), *Eucordyceps* (255 spp.), and *Neocordyceps* (8 spp.), but reduced the number of sections to seven. The subgeneric concept of his second revision [42] was not consistent with the previous revision [37]; for example, *C. sinensis* was classified in the subgenus *Ophiocordyceps* in the previous revision, but was transferred to the subgenus *Eucordyceps* in his second revision. Currently, around 400 entomopathogenic and mycoparasitic species are estimated in *Cordyceps s. l.* [25].

The revisionary work continued until the 1980s. Two new subgenera were added to *Cordyceps*; a new subgenus, *Bolacordyceps* O. E. Erikss., was proposed to include species that produce bola-ascospores, e.g., *C. bifusispora* O. E. Erikss. [43], whereas Zhang *et al.* [44] established a new subgenus, *Megalocordyceps* K. Zhang, C. Wang et M. Yan, to include species with unicellular ascospores, e.g., *C. gansuensis* K. Zhang, C. Wang & M. Yan (current name *Ophiocordyceps gansuensis* (K. Zhang, C. Wang & M. Yan) G. H. Sung *et al.*). However, the identification of *O. gansuensis* is questionable and is also considered a synonym of *O. sinensis* [45].

In addition, new genera were erected to include *Cordyceps* species with abnormal characters. For example, two new genera, *Sphaerocordyceps* Kobayasi and *Wakefieldiomyces* Kobayasi, were erected to incorporate *Cordyceps* species having atypical ascospores [46]. *Cordyceps palustris* Berk. & Broome (= *C. hormospora* Möller) and *C. ussuriensis* Koval were transferred to *Sphaerocordyceps* due to their spherical secondary ascospores, whereas *C. peltata* Wakef. was transferred to *Wakefieldiomyces* based on the constriction at the middle of the filamentous ascospores and their

subsequent division into two septate fragments.

Among the subgenera of *Cordyceps* s. l., the subgenus *Eucordyceps* Kobayasi [37, 42] is the largest (Table 4). However, Sung *et al.* [25] showed that the subgenera of *Cordyceps* (Table 4) were not only phylogenetically distant, but that their morphological characters, including those of their hosts, were also evolutionarily unrelated. Thus, the generic concept of *Cordyceps* Fr. was emended. As a result, the species of *Cordyceps* s. l. were reshuffled among four phylogenetic genera: 1) *Cordyceps* Fr. emend. G.H. Sung *et al.* (40 spp.) (*Cordycipitaceae* Kreisel ex G. H. Sung *et al.*); 2) *Ophiocordyceps* Petch emend. G. H. Sung *et al.* (146 spp.); 3) *Elaphocordyceps* G. H. Sung & Spatafora (21 spp.) (*Ophiocordycipitaceae*); and 4) *Metacordyceps* G. H. Sung *et al.* (6 spp.) (*Clavicipitaceae* (Lindau) Earle ex Rogerson). Among the four phylogenetic genera, *Ophiocordyceps* is the largest and is comprised of species distributed in all three morphological subgenera of Kobayasi [37, 42], indicating that the subgenera are polyphyletic. Recently, another phylogenetic genus, *Tyrannicordyceps* Kepler & Spatafora (*Clavicipitaceae*), was erected to accommodate six species of *Cordyceps* s. l. [47]. While nearly 175 species remain in the residual group of *Cordyceps* s. l. in *Cordycipitaceae* and many more species were missing from the phylogenetic analyses of Sung *et al.* [25], there is a high likelihood of establishing new phylogenetic genera in the future to accommodate those in the residual group as well as the missing ones. For example, *Polycephalomyces* Kobayasi was recently emended [48] to incorporate three residual *Cordyceps* species of Sung *et al.* [25] and four *Ophiocordyceps* species.

CONCLUSIONS

The present review of *Cordyceps* species s. l. highlights the old and deserted generic names given in the literature of the pre-Linnaean era as well as the generic synonyms associated with this genus in the post-Linnaean era. The genus *Cordyceps* has firmly stood against all its synonyms and has been used for approximately 200 years since its publication in 1818, proving itself as the oldest valid genus in *Cordycipitaceae*. *Cordyceps*, as a teleomorph fungus, has a clear generic concept based on characters such as peritheium, ascus, ascospore, part-spore, position of perithecia on stroma from lateral to apical, perpendicular to oblique, or superficial to immersed, and host specificity, among others [37, 38, 42]. Furthermore, *Cordyceps* is a traditionally used generic name for numerous medicinal insect fungi, especially in the eastern Asian countries [49, 50]. Recent amendment to Article 59 of the Melbourne Code has proposed protecting a single genus name for each fungal clade among the competing names on a priority basis, irrespective of the teleomorph or anamorph states of the organisms [51-55]. *Cordyceps* Fr., being the oldest valid genus name in the *Cordyceps* s. s. clade, ranks as the most preferred name over its competing names on the priority basis. Shrestha *et al.* [56] has recently discussed

the phylogenetic relationship between *Cordyceps* Fr. and *Beauveria* Vuill. in connection with the nomenclatural issue of these two genera.

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